

Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea

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Interannual dynamics (1959–1999) of calanoid copepods *Pseudocalanus elongatus*, *Temora longicornis* and *Acartia* spp. in the Central Baltic Sea are described for different life-stages. Using principal component (PCA) and correlation analysis the association of the stage-specific abundance to salinity and temperature was investigated. *P. elongatus* dynamics were related to high salinities in spring favouring maturation and reproduction. Additionally, low temperatures appear to be favourable for reproduction, whereas intermediate copepodite stages were positively correlated to temperature. *T. longicornis* and *Acartia* spp. life-stages were consistently associated with higher temperatures in spring. Furthermore, there are indications that *T. longicornis* maturation and reproductive success in summer is affected by salinity levels similarly to *P. elongatus*.

Keywords: *Acartia* spp., Central Baltic Sea, copepod life-stages, *Pseudocalanus elongatus*, salinity, stock dynamics, *Temora longicornis*, temperature.

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Introduction

Mesozooplankton species, especially calanoid copepods, play an important role in the Baltic Sea ecosystem. Changes in the species composition have been shown to influence the growth of their major predators, the clupeid fish herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (e.g. Flinkman *et al.*, 1998). Recent individual-based modelling approaches have demonstrated the dependence of larval survival and consequently recruitment of cod (*Gadus morhua*) on the dynamics of their main prey species (Hinrichsen *et al.*, 2002).

Long-term dynamics of copepod species have been investigated in different parts of the Baltic Sea, and their abundance and biomass were shown to depend to a large extent on hydrographic conditions (Ojaveer *et al.*, 1998; Viitasalo, 1992; Viitasalo *et al.*, 1995; Vuorinen and Ranta, 1987; Vuorinen *et al.*, 1998; Möllmann *et al.*, 2000) controlled by climatic factors (Dippner *et al.*, 2000, 2001; Hänninen *et al.*, 2000). In the Central Baltic basins especially, decreasing salinities since the late 1970s, caused by

increased river run-off (Bergström and Carlsson, 1994) and lower frequency of pulses of saline water intrusions from the North Sea and Skagerrak (Matthäus and Franck, 1992; Matthäus and Schinke, 1994) caused a declining biomass of *Pseudocalanus elongatus*, the dominant copepod in the area (Dippner *et al.*, 2000; Möllmann *et al.*, 2000). Two other important species, *Temora longicornis* and *Acartia* spp., were found to depend mainly on the prevailing temperature conditions in spring; *Acartia* spp. in particular showed a general increase in biomass in the 1990s, concurrent with prevailing relatively high temperature (Möllmann *et al.*, 2000).

Former studies from the Central Baltic investigated trends in total standing stocks of copepod species, while no stage-specific dynamics were considered. The latter may result in the identification of a critical life-stage or population dynamic processes driving the dynamics. Here we explored the stage-specific long-term dynamics of *P. elongatus*, *T. longicornis*, and *Acartia* spp. in the combined area of the Gdańsk Deep and the central Gotland Basin (Figure 1) and their association with temperature

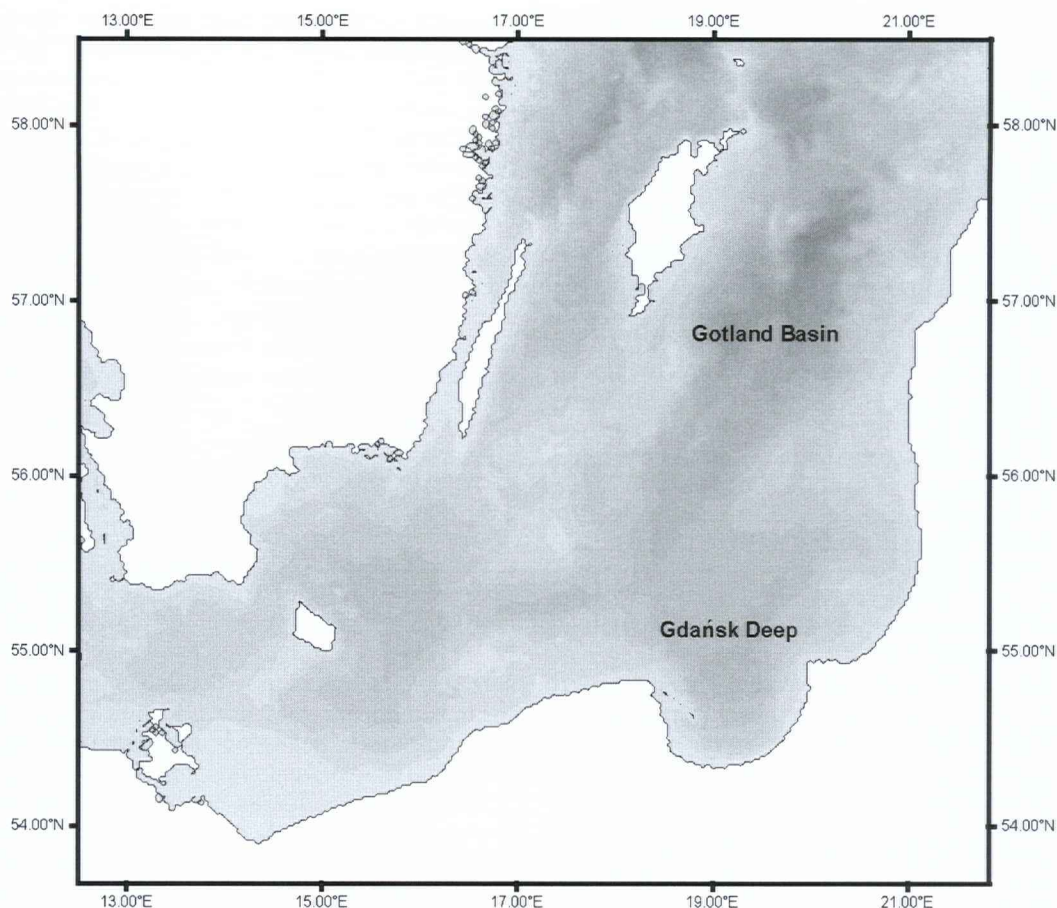


Figure 1. Map of the Central Baltic Sea with the area of investigation, i.e. the Gdańsk Deep and the Gotland Basin.

and salinity by using principal component (PCA) and correlation analysis.

Material and methods

Temperature and salinity

Temperature and salinity were measured by the Latvian Fisheries Research Institute (LATFRI) in Riga at 8 stations covering the Gdańsk Deep and the Central Gotland Basin. Measurements were performed during several cruises from 1961 to 1999 using a water sampler (Nansen type; 11 capacity) in 5 or 10-m steps. A Deep Sea Reversing Thermometer was used for temperature measurements, whereas salinity was measured either by the Knudsen Method (until 1992) or with an Inductivity Salinometer (since 1993).

Average values of temperature and salinity per season were calculated for the depth range 0–50 m, being the water layer mainly inhabited by *T. longicornis* and *Acartia* spp. (Sidrevics, 1979, 1984). As *P. elongatus*, especially the older stages, show a deeper distribution (Sidrevics, 1979 and 1984), the

layer between 50 and 100 m was also considered for this species.

Copepod stage-specific abundance

Copepod abundance data were collected during seasonal surveys of LATFRI, i.e. mainly in February, May, August, and November (later called winter, spring, summer, and autumn, respectively) conducted from 1959 to 1999. Sampling was performed mostly in the daytime using a Jeddy Net (UNESCO Press, 1968) operating vertically with a mesh size of 160 μ m and an opening diameter of 0.36 m. The gear is considered to quantitatively catch all copepodite stages as well as adult copepods, whereas nauplii may be underestimated (Anon., 1979).

Individual hauls were carried out in vertical steps, resulting in full coverage of the water column to a depth of 100 m at every station. For the present analysis, data from LATFRI stations in the Gdańsk Deep and the Central Gotland Basin were used. Each sample was divided into two subsamples. A mean value was calculated from both subsamples to derive the number per m^3 . Nauplii (N), copepodites

I to V (CI–CV) as well as adult females (CVI-f) and males (CVI-m) of the species *P. elongatus*, *T. longicornis*, and *Acartia* spp. (including *A. bifilosa*, *A. longiremis*, and *A. tonsa*) were identified in the samples.

Numerical analyses

Data were log-transformed to stabilize the variance. Missing values in the original time-series were interpolated using a linear trend regression (Statsoft, 1996). Principal component analyses (PCA) for classification (Le Fevre-Lehoerff *et al.*, 1995) were conducted in order to investigate (i) differences in the time trends between the different copepod stages, and (ii) associations between specific stages and salinity and temperature. One PCA was performed for every season and species with eight biological descriptors (stages N, CI, CII, CIII, CIV, CV, CVI-f, CVI-m) as well as salinity and temperature as supplementary variables. Associations between the variables were displayed by correlations between the first two principal components.

Additionally, simple correlation analyses were performed for the main reproduction periods, i.e. spring for *P. elongatus* as well as spring and summer for *T. longicornis* and *Acartia* spp. To account for autocorrelation in the data, the degrees of freedom (d.f.) in the statistical tests were adjusted using the equation by Chelton (1984), modified by Pyper and Peterman (1998):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_j r_{XX}(j)r_{YY}(j) \quad (1)$$

where N^* is the “effective number of degrees of freedom” for the time-series X and Y , N is the sample size, and $r_{XX}(j)$ and $r_{YY}(j)$ are the autocorrelation of X and Y at lag j . The latter were estimated using an estimator by Box and Jenkins (1976):

$$r_{XX}(j) = \frac{\sum_{t=1}^{N-j} (X_t - \bar{X})(X_{t+j} - \bar{X})}{\sum_{t=1}^N (X_t - \bar{X})^2} \quad (2)$$

where \bar{X} is the overall mean. We applied approximately $N/5$ lags in Equation (1), which ensures the robustness of the method (Pyper and Peterman, 1998).

Results

Temperature and salinity

Temperature in the upper 50 m showed a rather high interannual variability (Figure 2). Three marked

peaks are visible in the winter and spring time-series: in the middle of the 1970s as well as in the early 1980s and 1990s. Fluctuations were less pronounced in the deeper water layer (50–100 m), but exhibited in general the same time-trend. Compared to the earlier decades, the 1990s appeared to be the warmest period.

The time-series on salinity are characterized by a fairly stable situation in the 1960s and 1970s. From the 1980s onwards salinity declined continuously in both depth layers. Whereas salinity increased again from the middle of the 1990s onwards in the lower depth layer, it declined further in the upper layer.

Pseudocalanus elongatus

The overwintering stock of *P. elongatus* is dominated by CIV and CV copepodites and additionally lower proportions of CIII and CVI (Figure 3). Peak reproduction takes place in spring, when mainly N and CI constituted the *P. elongatus* stock. In summer, these stages have developed further, resulting in a dominance of CII, CIII, and CIV. The overwintering stock builds up in autumn, comprising mainly CIII, CIV, and CV.

The time-series display a period of a high overwintering stock in the late 1970s to the middle of the 1980s. Before and after this period, abundance was low and decreased since the late 1980s. This development is also found in spring for CVI-f as well as for the dominating N and CI. The latter two stages, however, also showed a period of high abundance at the beginning of the time-series. All other copepodite stages experienced an undulating development during the observed period. In summer and autumn the dominating stages (CII–CV) again showed a peak abundance period in the 1970s and 1980s and a drastic decline during the 1990s.

PCAs revealed pronounced differences in the behaviour of the seasonally dominating stages in spring (Figure 6). A group comprising the adult (CVI) and the youngest stages (N, CI) is separated from the intermediate copepodites (CII–CV). Both groups also showed a different association to hydrography, with the first group being associated with salinity in both depth horizons and the second group being connected to temperature. Correlation analyses confirmed the pattern with significant positive associations between N and salinity as well as an indication of a relationship between CVI-f and salinity (Table 1A). In contrast, intermediate copepodite stages were significantly related to temperatures. A relatively high negative correlation between N and temperature, however, was not statistically significant.

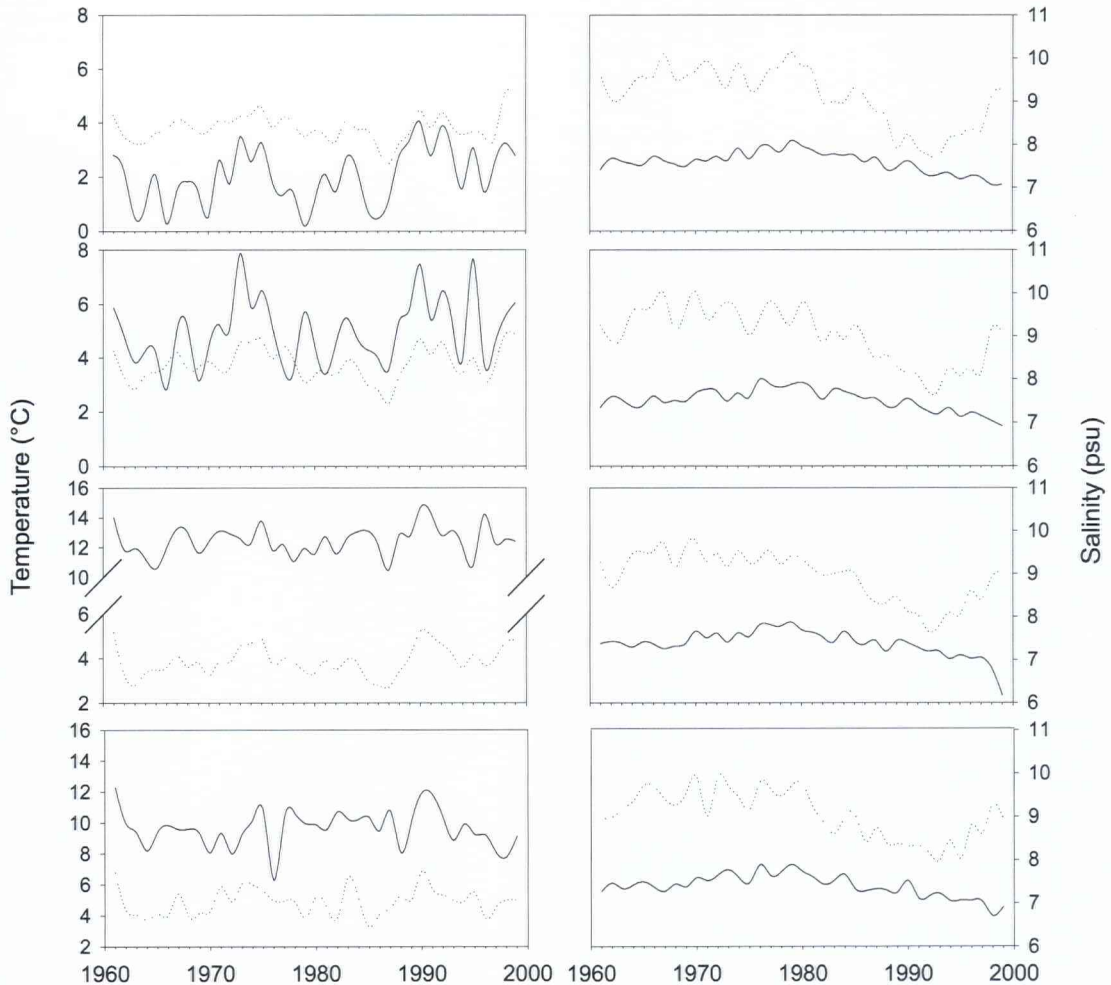


Figure 2. Seasonal time-series on temperature (left panels) and salinity (right panels); 1st row – winter, 2nd row – spring, 3rd row – summer, 4th row – autumn; solid line 0–50 m, dotted line 50–100 m.

Temora longicornis

T. longicornis hibernates mainly as CIV–CVI, although generally the overwintering stock is low compared to *P. elongatus* (Figure 4). Reproduction starts in spring and lasts throughout the year, as indicated by the continuous occurrence of N and the younger copepodite stages. Highest total abundance was found in summer, which coincides with the highest amount of CVI within the yearly cycle. In autumn, N and copepodites CI–CIV dominate with similar abundances.

The winter time-series showed increasing abundances of CIII–CV and CVI-f in the 1990s. Similarly in spring, exceptionally high standing stocks were observed for all stages from the late 1980s. Before the mid-1980s, spring abundances of all stages were low with an intermediate rise in the mid-1970s; however, only pronounced for N. Contrary to spring, the summer time-series is characterized by mainly

low and decreasing abundances in the 1990s with the exception of CIII–CV, which were relatively abundant. Generally a high variability is encountered in the summer time-series with high values at the beginning for N and copepodites, but lower ones for CVI. A similar high variability is found in autumn with peaks in the middle of the 1970s for N and CI–III and in the early 1980s for CIV–CV. In the 1990s, the standing stock of N and CI was low and on average higher for CII–CIV.

PCAs revealed no clear associations between the stage-specific abundance of *T. longicornis* and the hydrographic variables in winter and autumn (Figure 6). On the contrary, in spring, all stages had high positive correlations with the first principal axis, as was observed for temperature. In summer, no association with temperature was obvious, while all stages showed negative correlations to the second principal axis, as was found for salinity. Correlation

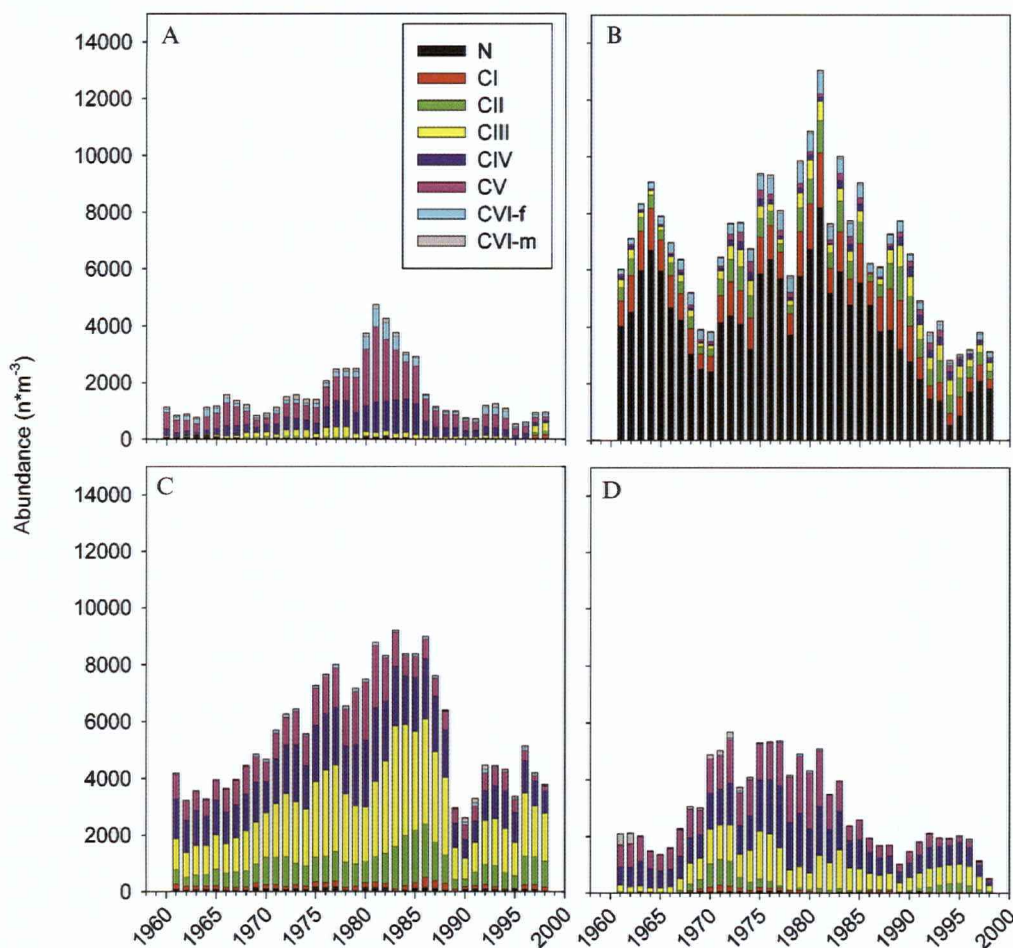


Figure 3. Seasonal time-series on stage-specific abundance of *Pseudocalanus elongatus*. Time-series are smoothed by a three-point running mean. (A) winter, (B) spring, (C) summer, (D) autumn.

analyses for the main reproductive periods confirmed a clear positive relationship between all stages and temperature in spring (Table 1B). The association to salinity is negative in spring, but significant only for CI and CII. In summer, correlations with salinity were positive but only significant for CI, CII, and CVI.

Acartia spp.

The seasonal dynamics of *Acartia* spp. are similar to those of *T. longicornis* (Figure 5). The overwintering stock is relatively small; reproduction starts in spring and lasts throughout the year. Peak abundance is in summer.

Increasing winter abundances of all stages were observed in the 1990s. Compared to *T. longicornis*, higher abundances of N and CVI-f of *Acartia* spp.

were encountered showing a wave-like development. Also in spring the time-trend was comparable to that of *T. longicornis*, i.e. with a marked increase in abundance since the late 1980s for all stages. Contrary to *T. longicornis*, this stepwise increase in standing stock was also encountered in summer and autumn, although mainly for CII and older stages.

Similarly to *T. longicornis*, PCAs for *Acartia* spp. showed only a weak association between hydrographic variables and stage-specific abundance in winter and autumn, as well as in summer (Figure 6). In spring, all stages were associated with temperature, whereas there is a clear opposition to salinity. Correlation analyses confirmed a clear positive and highly significant relationship of all stages to temperature in spring (Table 1C). The association to salinity is negative in spring (significant only for CIII and CIV) and in summer (significant only for CIII–CV).

Table 1A. Correlation tests between *Pseudocalanus elongatus* stage-specific abundance and temperature and salinity time-series. N^{eff} = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α).

Stage	Salinity			Temperature		
	N^{eff}	r	p	N^{eff}	r	p
N	13	0.61	<0.001*	26	-0.25	0.119
CI	16	0.31	0.056	28	0.10	0.562
CII	16	-0.08	0.627	29	0.43	0.006*
CIII	27	-0.15	0.352	35	0.48	0.002**
CIV	19	-0.11	0.491	29	0.64	<0.001**
CV	19	-0.07	0.670	27	0.50	0.001**
CVI-f	15	-0.41	0.009	23	0.05	0.748
CVI-m	21	-0.10	0.563	32	-0.14	0.399

*Significant at 0.05 and ** at 0.01 level.

Table 1B. Correlation tests between *Temora longicornis* stage-specific abundance and temperature and salinity time-series. N^{eff} = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α).

Stage	Spring						Summer					
	Salinity			Temperature			Salinity			Temperature		
	N^{eff}	r	p	N^{eff}	r	p	N^{eff}	r	p	N^{eff}	r	p
N	17	-0.17	0.302	31	0.63	<0.001**	22	0.38	0.018	34	0.16	0.317
CI	20	-0.44	0.005*	32	0.66	<0.001**	26	0.43	0.006*	34	0.03	0.835
CII	19	-0.46	0.003*	32	0.73	<0.001**	28	0.45	0.004*	36	-0.21	0.196
CIII	14	-0.47	0.003	28	0.66	<0.001**	26	0.25	0.129	35	-0.20	0.218
CIV	23	-0.34	0.033	34	0.60	<0.001**	29	0.07	0.680	37	-0.17	0.289
CV	19	-0.15	0.367	31	0.56	<0.001**	23	0.15	0.362	35	0.05	0.770
CVI-f	19	-0.31	0.055	32	0.35	0.028**	23	0.39	0.015*	34	0.10	0.548
CVI-m	21	-0.01	0.948	32	0.32	0.045**	18	0.54	<0.001*	31	-0.04	0.800

*Significant at 0.05 and ** at 0.01 level.

Table 1C. Correlation tests between *Acartia* spp. stage-specific abundance and temperature and salinity time-series. N^{eff} = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α).

Stage	Spring						Summer					
	Salinity			Temperature			Salinity			Temperature		
	N^{eff}	r	p	N^{eff}	r	p	N^{eff}	r	p	N^{eff}	r	p
N	18	-0.04	0.797	29	0.48	0.002**	22	0.19	0.240	32	0.19	0.244
CI	15	-0.39	0.013	29	0.44	0.005*	24	-0.01	0.990	32	0.27	0.097
CII	11	-0.41	0.009	26	0.55	<0.001**	22	-0.37	0.021	33	-0.03	0.860
CIII	15	-0.50	0.001*	29	0.44	0.005*	21	-0.43	0.007*	31	-0.14	0.399
CIV	14	-0.58	<0.001*	28	0.55	<0.001**	13	-0.58	<0.001*	26	-0.11	0.524
CV	16	-0.37	0.020	30	0.46	0.003**	14	-0.51	0.001*	27	-0.03	0.863
CVI-f	11	-0.43	0.006	26	0.63	<0.001**	19	-0.17	0.303	30	0.10	0.539
CVI-m	18	-0.33	0.042	32	0.50	0.001**	25	-0.17	0.301	34	-0.06	0.703

*Significant at 0.05 and ** at 0.01 level.

Discussion

Temperature and salinity

Hydrographic conditions in the Central Baltic Sea are mainly controlled by climatic factors (Dippner *et al.*, 2000, 2001; Hänninen *et al.*, 2000). The North Atlantic Oscillation (NAO), the dominant signal of

interannual variability in atmospheric circulation over Northern and Central Europe (e.g. Hurrell, 1995), has been clearly related to water temperature in the Central Baltic (Dippner *et al.*, 2000). Thus, the period of relatively high water temperatures in the 1990s was caused mainly by mild winters during the phase of high NAO in this period.

Similar to temperature, salinity in the Central Baltic is ultimately controlled by the large-scale

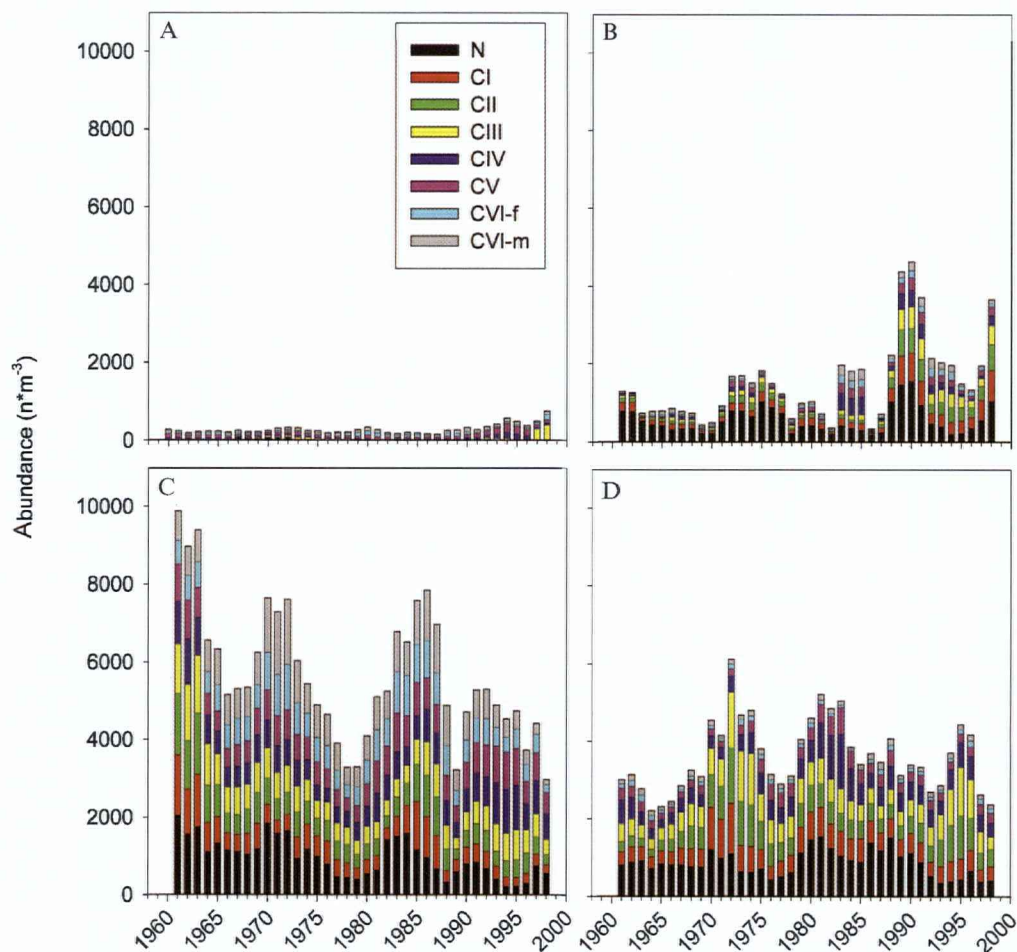


Figure 4. Seasonal time-series on stage-specific abundance of *Temora longicornis*. Time-series are smoothed by a three-point running mean. (A) winter, (B) spring, (C) summer, (D) autumn.

atmospheric circulation. A stronger meridional sea level pressure gradient over the North Atlantic since the 1980s resulted in an increase in rainfall and run-off, and consequently in reduced salinities at all depths (Zorita and Laine, 2000). Similarly, Hänninen *et al.* (2000) found a chain of events from NAO to freshwater run-off and deepwater salinity in the Gotland Basin. Salinity in and below the permanent halocline in the deep basins of the Central Baltic is mainly controlled by lateral advection of highly saline water from the North Sea (Matthäus and Franck, 1992; Matthäus and Schinke, 1994). The absence of these events between 1983 and 1993 was hypothesized to be due also to the changed atmospheric circulation along with intensified precipitation and run-off (Schinke and Matthäus, 1998; Hänninen *et al.*, 2000). The increase in salinity in the deep layer, observed in the presented time-series, was clearly a result of the last major inflow event in 1993.

Pseudocalanus elongatus

A clear stage-specific response of *P. elongatus* to the prevailing hydrographic conditions during the season of peak reproduction in spring is indicated. At this time of the year most of the CVI-f mature, and their number depends upon the size of the overwintering stock, which is dependent upon salinity. If salinity is low, fewer individuals reach the CV-stage in winter and are available for maturation in spring. Consequently, egg production and recruitment of N is low. A possible reason for this might be that low salinities cause osmotic stress and thus a higher energy requirement for this marine species. This may have resulted in retarded development and also lower egg production.

The development of the intermediate stages CII–CV in spring, and thus the development of older stages, is highly dependent on temperature; higher temperatures accelerate development times.

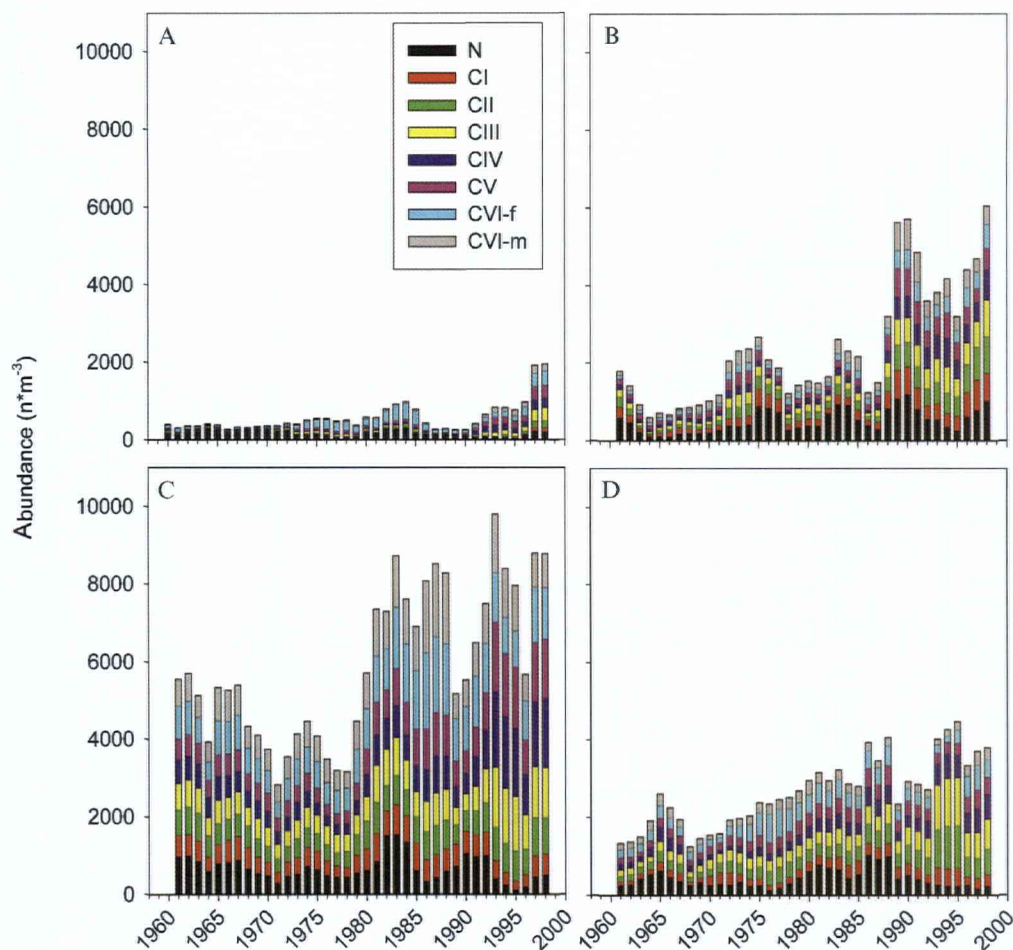


Figure 5. Seasonal time-series on stage-specific abundance of *Acartia* spp. Time-series are smoothed by a three-point running mean. (A) winter, (B) spring, (C) summer, (D) autumn.

However, as *P. elongatus* has only one generation in the Central Baltic (Line, 1979, 1984), the long-term dynamics of this species were triggered by the magnitude of the CVI-f stock formed in spring, which depends mainly on salinity. The peak recruitment period from the middle of the 1970s to the early 1980s is obviously caused by high salinity. This peak in reproduction is carried through the rest of the year and determines the overwintering stock. With decreasing salinities in the last two decades the abundance of CVI-f decreased and so did N. Contradicting this, a period of high N abundance and relatively low CVI-f numbers was encountered during the 1960s. A possible explanation may be that low temperatures in this period favoured reproduction (Möllmann *et al.*, 2000). This is indicated by the negative correlation of N with temperature in spring, although it is not statistically significant.

Temora longicornis

In contrast to *P. elongatus*, all life-stages of *T. longicornis* showed a uniform association with higher temperatures in spring. For this copepod species, which has up to five generations per year (Line, 1979, 1984), the building up of the population in spring is obviously strongly dependent on the warming of upper water layers. Thus, the drastic increase in spring standing stocks during the 1990s appears to be coupled to the high water temperatures accelerating development times. The increase in winter standing stocks in the 1990s may be related to an earlier onset of the warming.

A further mechanism may be the activation of resting eggs due to the spring rise in temperature. *T. longicornis* is known to produce these dormant stages to overcome low winter temperatures (Madhupratap *et al.*, 1996). Although the eggs have until now only been found in the North Sea (Lindley,

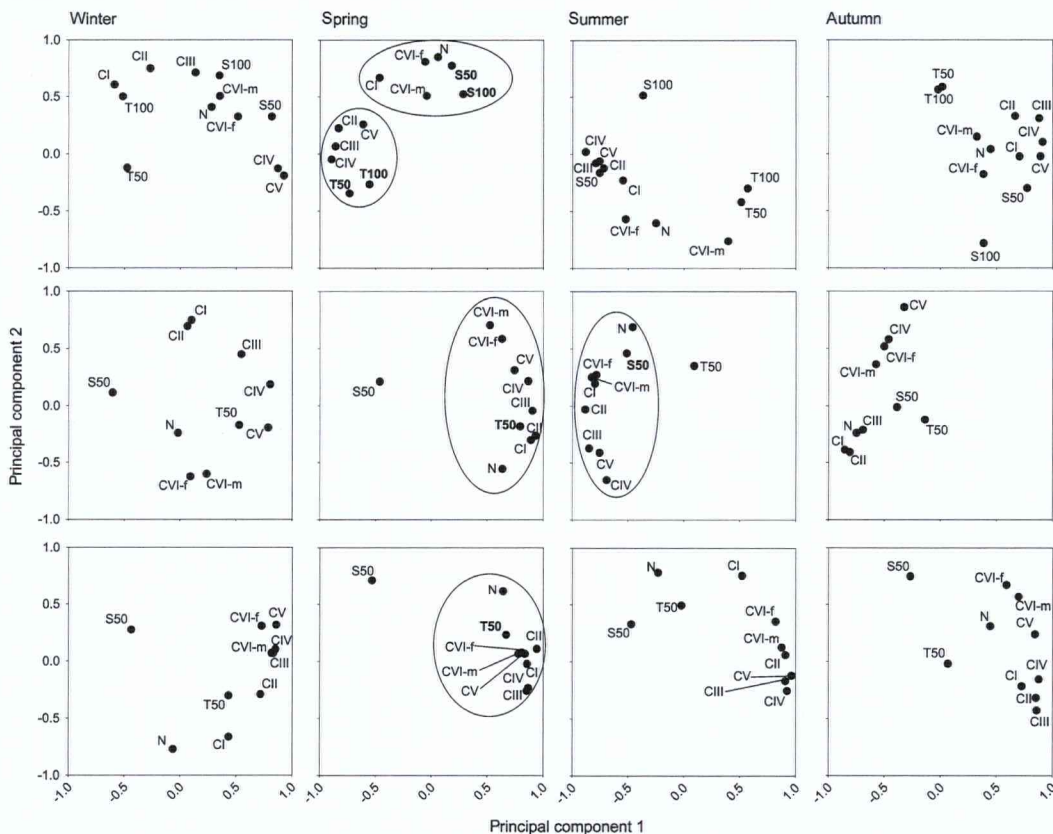


Figure 6. Results of principal component analyses (PCA): Correlation between the first 2 principal components per season and copepod species: 1st row – *Pseudocalanus elongatus*, 2nd row – *Temora longicornis*, 3rd row – *Acartia* spp.; T50 and S50 – average temperature and salinity in 0–50 m depth; T100 and S100 – average temperature and salinity in 50–100 m depth.

1986), it is very likely that they also occur in the Baltic (Madhupratap *et al.*, 1996).

The negative correlation of all stages with salinity in spring, although significant only for CI and CII, can be considered a result of the opposite development of temperature and salinity. To test this, additional multiple linear regression analyses were performed with temperature and salinity as independent variables, and the stage-specific abundance of *T. longicornis* as the dependent variable. Partial correlation coefficients for both independent variables were all highly significant for temperature ($p < 0.01$), whereas for salinity significant ($p < 0.05$) partial correlation coefficients were only found for CI, CII, and CIII. In all these cases coefficients for temperature were higher than for salinity, confirming temperature to be the most influential variable. We consider this finding reasonable, as *T. longicornis* is a species of marine origin not favouring explicitly low saline conditions (Raymont, 1983).

In summer the association to salinity was positive. Interestingly, significant correlations could be found only for CVI and the early stages CI and CII (with N being almost significant). Obviously maturation

and consequently reproductive success of *T. longicornis* in summer, when temperature is generally sufficiently high, suffers similarly to *P. elongatus* from low salinities. The general decrease in summer abundance may thus be caused by the decreasing salinity.

Acartia spp.

The group of *Acartia* species has a similar life-cycle as *T. longicornis* with up to seven generations per year (Line, 1979, 1984) and PCAs as well as correlation analyses also revealed for *Acartia* spp. the significant association of all stages with temperature in spring. For *Acartia* spp., the beginning of population development is obviously also strongly dependent on spring warming, which explains the drastic increase in abundance during the warm 1990s. The activation of resting eggs, which is known to occur in the Baltic (Katajisto *et al.*, 1998; Madhupratap *et al.*, 1996; Viitasalo and Katajisto, 1994), may be especially important for this copepod.

Negative correlations with salinity were found again in spring and, in contrast to *T. longicornis*, in

summer. This suggests that reproduction of *Acartia* spp. in either season is favoured by lower salinities. To test whether the significant negative correlations with salinity are only due to the mainly opposite trend of the hydrographic variables, as found for *T. longicornis*, multiple linear regression analyses were conducted. As for *T. longicornis*, highly significant ($p < 0.01$) partial correlation coefficients in spring were found for temperature and all stages, whereas for salinity highly significant ($p < 0.01$) coefficients were derived only for CIII and CIV, and significant ($p < 0.05$) ones only for CII and CVI. In contrast, for summer, highly significant ($p < 0.01$) negative partial correlation coefficients were observed for CIII to CV and salinity, whereas coefficients for temperature were not significant. These results confirm that, in spring, temperature is the limiting factor, although lower salinities are favourable for *Acartia* spp.; this is especially true for summer.

The difference in summer response to salinity between *Acartia* spp. and *T. longicornis* is clearly visible in the time-series. A generally high abundance was found for *Acartia* spp. during the 1990s, whereas the standing stock of *T. longicornis* decreased.

Conclusions

Investigations of the long-term stage-specific dynamics of major Central Baltic copepod species provide new insights into the effects of hydrography. The study confirmed the impact of salinity during maturation and reproduction in spring on the stock development of *P. elongatus* (Möllmann *et al.*, 2000), but additionally a stage-specific response to temperature was detected. While lower temperatures are favourable for reproduction, the development of intermediate copepodite stages is accelerated by warmer conditions. The dynamics of *T. longicornis* and *Acartia* spp. are mainly related to temperature in spring as previously demonstrated (Dippner *et al.*, 2000; Möllmann *et al.*, 2000). Additionally, we show that in summer, when temperature is not critical, higher salinities favour the maturation and subsequent reproduction of *T. longicornis*, similar to *P. elongatus*.

In addition to hydrography, predation by planktivores (e.g. Rudstam *et al.*, 1994) may contribute to copepod dynamics. In particular, the drastically enlarged sprat stock (Köster *et al.*, 2001) may have the potential to control the stock of *P. elongatus* and *T. longicornis* (Möllmann and Köster, 1999, 2002). Also food availability can influence copepod dynamics, especially moulting and egg production (e.g. Berggreen *et al.*, 1988). In relation to this, competition between the copepod species may play a role. *Acartia* spp. may have taken advantage of the decreasing standing stock of *P. elongatus*, which may have contributed to the drastic increase in

abundance. This issue needs further investigation, but unfortunately, to our knowledge, no reliable time-series on phytoplankton standing stocks are available for the area. Nevertheless, we believe that the main time-trends of the considered copepod species are explainable mainly by temperature and salinity changes.

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References

- Anon. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. In: Hernroth, L. (Ed.), Baltic Marine Biologists. 15 pp.
- Berggreen, U., Hansen, B., and Kjørboe, T. 1988. Food size spectra ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Marine Biology, 99: 341–352.
- Bergström, S., and Carlsson, B. 1994. River runoff to the Baltic Sea 1950–1990. Ambio, 23: 4–5.
- Box, G. E. P., and Jenkins, G. W. 1976. Time Series Analysis: Forecasting and Control. Holden-Day, San Francisco, CA. xxi + 575 pp.
- Chelton, D. B. 1984. Commentary: short-term climate variability in the Northeast Pacific Ocean: in the influence of ocean conditions on the production of salmonids in the North Pacific, pp. 87–99. Edited by W. Pearcy. Oregon State University Press, Corvallis, Oregon, USA.
- Dippner, J. W., Hänninen, J., Kuosa, H., and Vuorinen, I. 2001. The influence of climate variability on zooplankton abundance in the northern Baltic Archipelago Sea (SW Finland). ICES Journal of Marine Science, 58: 569–578.
- Dippner, J. W., Kornilovs, G., and Sidrevics, L. 2000. Long-term variability of mesozooplankton in the Central Baltic Sea. Journal of Marine Systems, 25: 23–32.
- Flinkman, J., Aro, E., Vuorinen, I., and Viitasalo, M. 1998. Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s. Top-down and bottom-up processes at work. Marine Ecology Progress Series, 165: 127–136.
- Hänninen, J., Vuorinen, I., and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnology and Oceanography, 45: 703–710.
- Hinrichsen, H.-H., Möllmann, C., Voss, R., Köster, F. W., and Kornilovs, G. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. Submitted to Canadian Journal of Fisheries and Aquatic Sciences.

- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation and regional temperature and precipitation. *Science*, 269: 676–679.
- Katajisto, T., Viitasalo, M., and Koski, M. 1998. Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. *Marine Ecology Progress Series*, 163: 133–143.
- Köster, F. W., Möllmann, C., Neuenfeldt, S., St. John, M. A., Plikshs, M., and Voss, R. 2001. Developing Baltic cod recruitment models. I: Resolving spatial and temporal dynamics of spawning stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1516–1533.
- Le Fevre-Lehoerff, G., Ibanez, F., Poniz, P., and Fromentin, J. M. 1995. Hydroclimatic relationships with planktonic time series from 1975 to 1992 in the North Sea off Gravelines, France. *Marine Ecology Progress Series*, 129: 269–281.
- Lindley, J. A. 1986. Dormant eggs of calanoid copepods in sea-bed sediments of the English Channel and southern North Sea. *Journal of Plankton Research*, 8: 399–400.
- Line, R. J. 1979. Some observations on fecundity and development cycles of the main zooplankton species in the Baltic Sea and the Gulf of Riga. In: *Fisheries investigations in the basin of the Baltic Sea*. Riga, Zvaigzne, 14: 3–10. (In Russian.)
- Line, R. J. 1984. On reproduction and mortality of zooplankton (Copepoda) in the south-eastern, eastern and north-eastern Baltic. In: *Articles on Biological Productivity of the Baltic Sea*. Moscow, 2: 265–274. (In Russian.)
- Madhupratap, M., Nehring, S., and Lenz, J. 1996. Resting eggs of zooplankton (Copepoda and Cladocera) from the Kiel Bay and adjacent waters (southwestern Baltic). *Marine Biology*, 125: 77–87.
- Matthäus, W., and Franck, H. 1992. Characteristics of major Baltic inflows: a statistical analysis. *Continental Shelf Research*, 12: 1375–1400.
- Matthäus, W., and Schinke, H. 1994. Mean atmospheric circulation patterns associated with major Baltic inflows. *Deutsche Hydrographische Zeitschrift*, 46: 321–339.
- Möllmann, C., and Köster, F.W. 1999. Food consumption by clupeids in the Central Baltic: evidence for top-down control? *ICES Journal of Marine Science*, 56 (Suppl): 100–113.
- Möllmann, C., and Köster, F. W. 2002. Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *Journal of Plankton Research*. (In press.)
- Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *Journal of Plankton Research*, 22: 2015–2038.
- Ojaveer, E., Lumberg, A., and Ojaveer, H. 1998. Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES Journal of Marine Science*, 55: 748–755.
- Pyper, B. J., and Peterman, R. M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 2127–2210.
- Raymont, J. E. G. 1983. *Plankton and Productivity in the Oceans*, 2nd edn, vol. 2: Zooplankton. Pergamon Press. 824 pp.
- Rudstam, L. G., Aneer, G., and Hildén, M. 1994. Top-down control in the pelagic Baltic ecosystem. *Dana*, 10: 105–129.
- Schinke, H., and Matthäus, W. 1998. On the causes of major Baltic inflows and analysis of long time series. *Continental Shelf Research*, 18: 67–97.
- Sidrevics, L. L. 1979. Some peculiarities of vertical distribution of zooplankton in the Central Baltic. In: *Fisheries investigations in the basin of the Baltic sea*. Riga, Zvaigzne, 14: 11–19. (In Russian.)
- Sidrevics, L. L. 1984. The main peculiarities of zooplankton distribution in the South-eastern, Eastern and North-eastern Baltic. In: *Articles on Biological Productivity of the Baltic Sea*. Moscow, 2: 172–187. (In Russian.)
- Statsoft. 1996. *STATISTICA for Windows*. StatSoft Inc., Tulsa, USA.
- UNESCO Press. 1968. *Zooplankton sampling*. Monographs on Oceanographic Methodology, 2. 174 pp.
- Viitasalo, M. 1992. Mesozooplankton in the Gulf of Finland and Northern Baltic proper: a review of monitoring data. *Ophelia*, 35: 147–168.
- Viitasalo, M., and Katajisto, T. 1994. Mesozooplankton resting eggs in the Baltic Sea: identification and vertical distribution in laminated and mixed sediments. *Marine Biology*, 120: 455–465.
- Viitasalo, M., Vuorinen, I., and Saesmaa, S. 1995. Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research*, 17: 1857–1878.
- Vuorinen, I., and Ranta, E. 1987. Dynamics of marine mesozooplankton at Seili, Northern Baltic Sea, in 1967–1975. *Ophelia*, 21: 31–48.
- Vuorinen, I., Hänninen, J., Viitasalo, M., Helminen, U., and Kuosa, H. 1998. Proportion of copepod biomass declines together with decreasing salinities in the Baltic Sea. *ICES Journal of Marine Science*, 55: 767–774.
- Zorita, E., and Laine, A. 2000. Dependence of salinity and oxygen concentrations in the Baltic Sea on large-scale atmospheric circulation. *Climate Research*, 14: 25–41.